

Carbon inputs regulate the temperature sensitivity of soil respiration in temperate forests

LIU Yulin^{1,2}, LI Jiwei^{1,2}, HAI Xuying³, WU Jianzhao³, DONG Lingbo³, PAN Yingjie^{1,2}, SHANGGUAN Zhouping^{1,2,3}, WANG Kaibo^{4*}, DENG Lei^{1,2,3*}

¹ State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China;

² University of Chinese Academy of Sciences, Beijing 100049, China;

³ Institute of Soil and Water Conservation, Northwest Agriculture and Forestry University, Yangling 712100, China;

⁴ State Key Laboratory of Loess and Quaternary Geology, Institute of Earth Environment, Chinese Academy of Sciences, Xi'an 710075, China

Abstract: Litter and root activities may alter the temperature sensitivity (Q_{10}) of soil respiration. However, existing studies have not provided a comprehensive understanding of the effects of litter and root carbon inputs on the Q_{10} of soil respiration in different seasons. In this study, we used the trench method under in situ conditions to measure the total soil respiration (R_{total}), litter-removed soil respiration ($R_{no-litter}$), root-removed soil respiration ($R_{no-root}$), and the decomposition of soil organic matter (i.e., both litter and root removal; $RsOM$) in different seasons of pioneer (*Populus davidiana* Dode) and climax (*Quercus liaotungensis* Mary) forests on the Loess Plateau, China. Soil temperature, soil moisture, litter biomass, fine root biomass, litter carbon, and root carbon were analyzed to obtain the drive mechanism of the Q_{10} of soil respiration in the two forests. The results showed that the Q_{10} of soil respiration exhibited seasonality, and the Q_{10} of soil respiration was higher in summer. The litter enhanced the Q_{10} of soil respiration considerably more than the root did. Soil temperature, soil moisture, fine root biomass, and litter carbon were the main factors used to predict the Q_{10} of different soil respiration components. These findings indicated that factors affecting the Q_{10} of soil respiration highly depended on soil temperature and soil moisture as well as related litter and root traits in the two forests, which can improve our understanding of soil carbon-climate feedback in global warming. The results of this study can provide reference for exploring soil respiration under temperate forest restoration.

Keywords: litter biomass; root carbon; soil respiration; temperate forests; Loess Plateau

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1 Introduction

A forest ecosystem is the main carbon sequestration body (Kukumägi et al., 2017) that accounts for 80% of global soil carbon pools (He et al., 2021). Soil CO₂ efflux presents the largest carbon flux between terrestrial ecosystems and the atmosphere, which is important for the carbon cycle in forest ecosystem (Bond-Lamberty and Thomson, 2010; Ballantyne et al., 2015). The annual emission of CO₂ from soils into the atmosphere accounts for 5%–20% of the greenhouse gas emitted (Wang et al., 2019), which is the key factor leading to global warming. The temperature

*Corresponding authors: DENG Lei (Email: leideng@ms.iswc.ac.cn); WANG Kaibo (Email: wangkb@ieecas.cn)

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sensitivity (Q_{10}) of soil respiration is commonly used to estimate its feedback strength for the temperature increase (Bond-Lamberty et al., 2018; Yan et al., 2019; Ge et al., 2020). Therefore, determining the Q_{10} of soil respiration is essential for predicting soil carbon pools and their potential effects on climate change (Todd-Brown et al., 2013; Bond-Lamberty et al., 2018).

Soil CO_2 emissions are derived from the metabolism of plant roots (autotrophic respiration, R_a) and microbial communities (heterotrophic respiration, R_h) (Kukumägi et al., 2017; Zhang et al., 2021), and it is important to determine the contribution of each component to soil respiration and its dependence on multiple environmental factors (Wang et al., 2019; Ge et al., 2020). Vegetation controls soil respiration and its components by influencing litter and root biomass, nutrient availability, soil temperature, and soil moisture (Deng et al., 2014a, 2018; Li et al., 2020). On a large spatial scale, the length of the plant growth season is a chief driving factor for soil respiration (Davidson et al., 2006; Uri et al., 2012; Varik et al., 2013; Machmuller et al., 2018). Moreover, for various seasonal scales, the Q_{10} of soil respiration shows different influencing factors (Davidson et al., 2006; Ferreira et al., 2016). For example, seasonal changes in the root activity trigger environmental factors that have a considerable effect on R_a (Li et al., 2020a); and substrates decompose through heterotrophic soil organisms, whose number and nutrient availability vary with substrates (such as litter) and seasonal variations, respectively (Luan et al., 2011; Ma et al., 2014).

The forest type is another important factor that leads to the change in the Q_{10} values of R_a and R_h (Wang et al., 2016; Yu et al., 2017). Studies have shown that various forest types have different effects on the Q_{10} values of total soil respiration (R_{total}), R_a , and R_h (Wang et al., 2013) and that the Q_{10} values of both R_a and R_h are significantly positively influenced by forest types (Yu et al., 2017; Li et al., 2020a). However, other studies have reported that no significant difference exists between forest types and the Q_{10} of rhizosphere respiration (Shi et al., 2015). Therefore, there is no consensus on how forest types affect the Q_{10} values of R_{total} , R_a , and R_h . Separately studying the Q_{10} values of R_a and R_h changes is crucial and could enhance our understanding of total soil respiration changes (Gaumont-Guay et al., 2009; Chang et al., 2016).

Populus davidiana Dode (pioneer) forests and *Quercus liaotungensis* Mary (climax) forests are typical natural secondary forests species available in the Ziwuling forests region situated on the Chinese Loess Plateau (Deng et al., 2014b). In the two forests, we set up four treatments, namely R_{total} , litter-removed soil respiration ($R_{\text{no-litter}}$), root-removed soil respiration ($R_{\text{no-root}}$), and the decomposition of soil organic matter (i.e., both litter and root removal; R_{SOM}), to observe the changes in soil respiration fluxes on different season scales; and then, seasonal dynamic changes and factors influencing the Q_{10} of soil respiration were obtained. The objectives of this study were to: (1) classify R_{total} , $R_{\text{no-litter}}$, $R_{\text{no-root}}$, and R_{SOM} to independently quantify the Q_{10} of soil respiration in different seasons in the two forests; (2) explore how the Q_{10} of R_{total} , $R_{\text{no-litter}}$, $R_{\text{no-root}}$, and R_{SOM} vary with forest types; and (3) reveal the main factors affecting the changes in the Q_{10} of soil respiration.

2 Materials and methods

2.1 Study area

This study was conducted at the Lianjiabian Forest Farmland ($36^{\circ}00'43''$ – $36^{\circ}06'55''\text{N}$, $108^{\circ}26'23''$ – $108^{\circ}41'10''\text{E}$; 1371–1453 m a.s.l.) in the Heshui County of Gansu Province, China, located in the Ziwuling forests region on the Loess Plateau (Deng et al., 2014b). The study area has a mid-temperate continental monsoon climate. The annual average temperature is 10°C and average annual precipitation is 587 mm (Liu et al., 2020). The study area has a typical loess hilly topography. As the main soil type, loessial soil (*Calcic Cambisols*) is developed from the primary or secondary loess parent materials, and is distributed evenly at a depth of 50–130 m (Wang et al., 2020). The study area is located in a temperate zone, with a forest density of 80%–95%. This area is suitable for the development of the deciduous broadleaved and temperate coniferous forest

species, such as *P. davidiana*, *Betula platyphylla* Suk., and *Q. liaotungensis*. All these species grow on the top of the hillside, and the slope of the hillside does not exceed 5° (Liu et al., 2020).

According to local forest farm records, vegetation almost disappeared because of human-caused destruction. After the local residents moved out around 1860, the vegetation based on abandoned farmlands naturally recovered, and the vegetation landscapes dominated by the secondary deciduous broadleaved forests formed gradually. Moreover, a relatively complete succession chronosequence of secondary vegetation, including abandoned farmland, herbage, shrub, pioneer forest, climax community, formed in this area. We selected *P. davidiana* forests and *Q. liaotungensis* forests in this study, which are approximately 110 and 160 years old, respectively (Deng et al., 2018; Wang et al., 2020). The main understory plants associated with *P. davidiana* included *Carex lanceolata* Boott, *Artemisia campestris* L., *Ulmus macrocarpa* Hance, *Acer ginnala* Maxim., *Armeniaca sibirica* (L.) Lam., and *B. platyphylla*. The understory plants associated with *Q. liaotungensis* comprised *C. lanceolata*, *A. campestris*, *P. davidiana*, and *B. platyphylla*.

2.2 Experimental design

Mature *P. davidiana* forests and *Q. liaotungensis* forests were selected in 2016. The two forests are situated within a distance of less than 2 km from each other. In October 2016, we performed a series of treatments at three plots (each plot is 30 m×30 m) in each forest, in which R_{total} , $R_{\text{no-litter}}$, $R_{\text{no-root}}$, and R_{SOM} were studied with five replicates per treatment. Root exclusion was performed using the trench method (Rey et al., 2002). An area of 1 m×1 m was selected and dug to a depth of 100 cm to remove the root systems. A 100-mesh nylon net was laid around it, and then, in the dug area, the soil was filled again. The soil respiration rate was measured each month from March to November (spring–autumn) in 2018; spring was from March to May, summer was from June to August, and autumn was from September to November.

2.3 Soil respiration measurements

The soil respiration rate was measured using a soil respiration monitoring system (LI-8100A, Li-COR Inc., Nebraska, USA). From March to November in 2018, at the end or beginning of each month, the soil respiration rate was measured between 09:00 and 14:00 (LST) during the day; the sunny weather was the condition preferred for analyses each time, with 3-min measurements for each chamber. To eliminate the influence of soil disturbance, weeds were cut a day before each measurement. The LI-8100 temperature and humidity sensor was used to simultaneously measure the soil temperature and soil volumetric water content at the depth of 5 cm.

2.4 Litter and root measurements

Fine root biomass (RB) was obtained after each soil respiration measurement. In each plot of the two forests, the soil surface mulch was cleaned, a root drill with 9-cm diameter was used to collect the RB at a soil depth of 0–10 cm, 5 drills for each plot were obtained in the diagonal direction, and the dry sieve method was employed to acquire the root system after mixing. At the same time, litter biomass (LB) was collected, and 10 litter collection frames with an area of 1 m×1 m were randomly set up in each sample site to determine LB. Leaves, fallen branches, fallen fruits, fallen flowers, miscellaneous branches, and miscellaneous fruits (worms and faeces, bird droppings, and plant debris) were separated from other parts and taken to the laboratory. The collected samples were dried in an oven at 80°C to obtain a constant weight, and then, were weighed. Litter carbon (LC) and root carbon (RC) were determined through wet digestion by using the $K_2Cr_2O_7$ oxidation method (Nelson and Sommers, 1982).

2.5 Data analysis and statistics

The Q_{10} values of soil respiration are evaluated using the following equations (Li et al., 2020b):

$$R_s = ae^{bT}, \quad (1)$$

$$Q_{10} = e^{10b}, \quad (2)$$

where R_s is the measured soil respiration rate ($\mu\text{mol}/(\text{m}^2\cdot\text{s})$); T is the measured soil temperature ($^{\circ}\text{C}$); and a and b are the fitted parameters.

Two-way analysis of variance (ANOVA) was used to obtain significant differences ($P<0.05$) among various treatments and seasons, followed by the least-significant difference (LSD) test, which was performed for the post hoc comparisons of means. Statistical significance was defined as $P<0.05$. We used linear models to analyse the effects of soil temperature and soil moisture on the Q_{10} values, and utilized the Pearson correlation analysis to determine the relationship of the Q_{10} values with LB, RB, LC, and RC. Structural equation model was performed to identify the possible pathways that allow variables to affect the Q_{10} of soil respiration in the two forests. The structural equation model was constructed using Amos 24.0. Other figures were drawn using SigmaPlot 12.5.

3 Results

3.1 Seasonal dynamics of the temperature sensitivity (Q_{10}) values under litter and root treatments

For all the treatments, summer was the season with the highest Q_{10} values in *P. davidiana* forests and *Q. liaotungensis* forests (Fig. 1). Among different seasons, the Q_{10} values in summer were considerably different from that in spring and autumn ($P<0.05$; Table 1). No significant difference was observed in the Q_{10} values between spring and autumn ($P>0.05$); however, the Q_{10} values in spring were higher than that in autumn. Overall, the Q_{10} values in *P. davidiana* forests significantly varied among different seasons and treatments ($P<0.01$), and both the seasons and treatments affected the Q_{10} values in *P. davidiana* forests ($P<0.05$; Table 1). The Q_{10} values in *P. davidiana* forests and *Q. liaotungensis* forests were 0.455–3.869 and 0.430–3.861, respectively (Fig. 1).

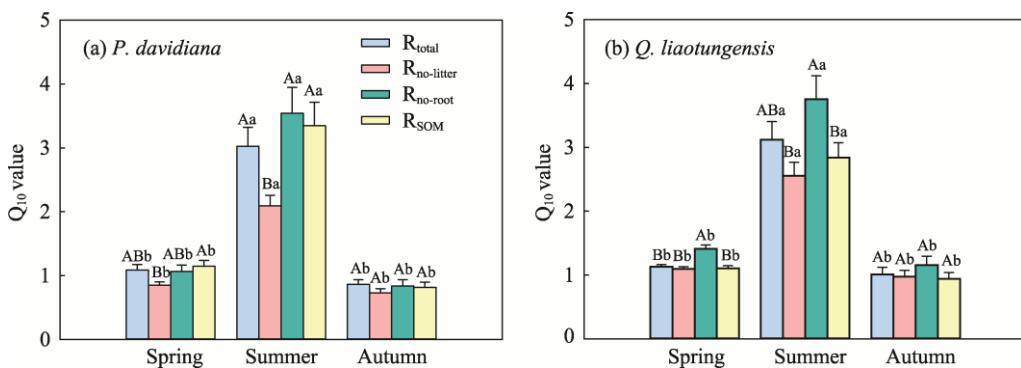


Fig. 1 Seasonal differences among the temperature sensitivity (Q_{10}) of total soil respiration (R_{total}), litter-removed soil respiration ($R_{\text{no-litter}}$), root-removed soil respiration ($R_{\text{no-root}}$), and the decomposition of soil organic matter (i.e., both litter and root removal; R_{SOM}) in *Populus davidiana* Dode forests (a) and *Quercus liaotungensis* Mary forests (b). Lowercase letters indicate the variations observed with changing seasons for the same treatment ($P<0.05$). Uppercase letters indicate the variations observed with varying treatments in the same season ($P<0.05$). Bars represent standard errors.

Table 1 Analysis of variance for the factors affecting the temperature sensitivity (Q_{10}) of soil respiration with seasons and treatments in *Populus davidiana* Dode forests and *Quercus liaotungensis* Mary forests

Factor	Degree of freedom	<i>P. davidiana</i>		<i>Q. liaotungensis</i>	
		Mean square	F value	Mean square	F value
Seasons	2	87.04	148.21***	77.50	166.89***
Treatments	3	3.28	5.58**	2.77	5.96**
Seasons×Treatments	6	1.60	2.72*	0.82	1.78

Note: *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

3.2 Relationships of the Q_{10} values with soil temperature and soil moisture under litter and root treatments

In all the treatments, the soil respiration rate and soil temperature showed a trend of first increased and then decreased. The maximum values of soil respiration and soil temperature both obtained in July in summer; however, the soil moisture was relatively lower in July (Fig. 2). The Q_{10} values were driven by soil moisture and soil temperature (Fig. 3; Table 2). The combined effect of soil temperature and soil moisture showed an extremely significant correlation with the Q_{10} values ($P < 0.001$; Fig. 3; Table 2). Regardless of the season, soil temperature showed a positive response to the Q_{10} values in *P. davidiana* forests and *Q. liaotungensis* forests, with the coefficient of determination (R^2) was above 0.80, and the promotion effect of soil temperature on the Q_{10} values were more obvious in summer (Fig. 4a and b). On the whole, soil moisture showed a negative response to the Q_{10} values (Fig. 4c and d).

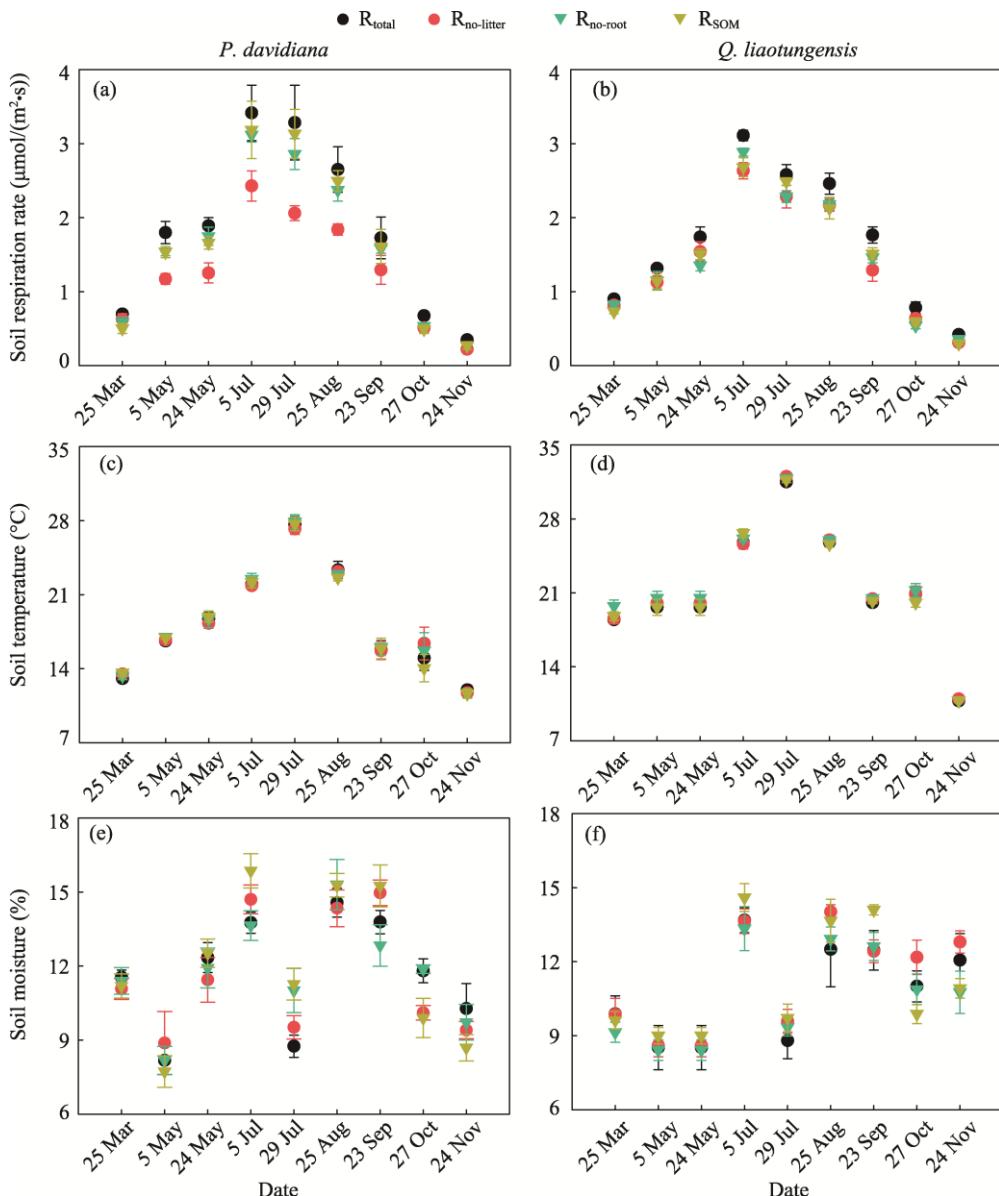


Fig. 2 Seasonal changes in soil respiration rate, soil temperature, and soil moisture in *P. davidiana* forests (a, c, and e) and *Q. liaotungensis* forests (b, d, and f). Bars represent standard errors.

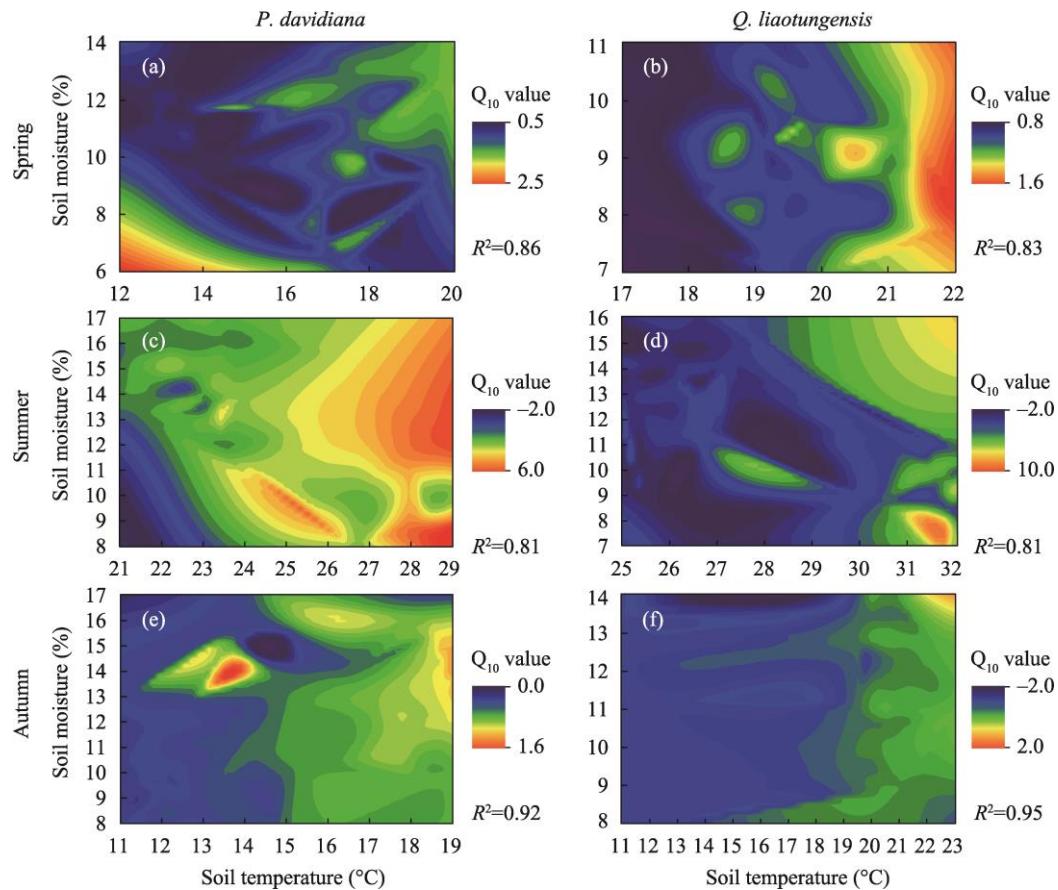


Fig. 3 Responses of the Q_{10} of soil respiration to the combination of soil temperature (T) and soil moisture (M) with a bivariate non-linear model ($Q_{10}=a\times M\times T+b\times M+c\times T+d$, where a , b , and c represent the coefficients of soil temperature and soil moisture, and d represents the constant) in *P. davidiana* forests (a, c, and e) and *Q. liaotungensis* forests (b, d, and f). The specific fitting equation is shown in Table 2.

Table 2 Equations of the Q_{10} of soil respiration with soil temperature (T) and soil moisture (M) in *P. davidiana* forests and *Q. liaotungensis* forests

Forests	Season	Equation	R^2
<i>P. davidiana</i>	Spring	$Q_{10}=0.01\times M\times T-0.21\times M-0.03\times T+1.41$	0.86***
	Summer	$Q_{10}=-0.01\times M\times T+0.38\times M+0.66\times T-14.56$	0.81***
	Autumn	$Q_{10}=0.005\times M\times T-0.07\times M+0.05\times T+0.07$	0.92***
<i>Q. liaotungensis</i>	Spring	$Q_{10}=-0.02\times M\times T+0.33\times M+0.30\times T-4.57$	0.83***
	Summer	$Q_{10}=-0.02\times M\times T+0.37\times M+0.49\times T-9.83$	0.81***
	Autumn	$Q_{10}=-0.001\times M\times T+0.02\times M+0.11\times T-0.81$	0.95***

Note: ***, $P<0.001$.

3.3 Relationships of the Q_{10} values with litter biomass (LB), fine root biomass (RB), litter carbon (LC), and root carbon (RC) under litter and root treatments

The LB of *Q. liaotungensis* forests was significantly higher than that of *P. davidiana* forests ($P<0.05$), and the LC of *P. davidiana* forests was significantly higher than that of *Q. liaotungensis* forests ($P<0.05$; Table 3). The RB and RC of *P. davidiana* forests attained the peak in autumn, and the RB of *Q. liaotungensis* forests was the highest in summer. No significant difference was observed in RB and RC between *P. davidiana* forests and *Q. liaotungensis* forests in the same season or different seasons ($P>0.05$; Table 3).

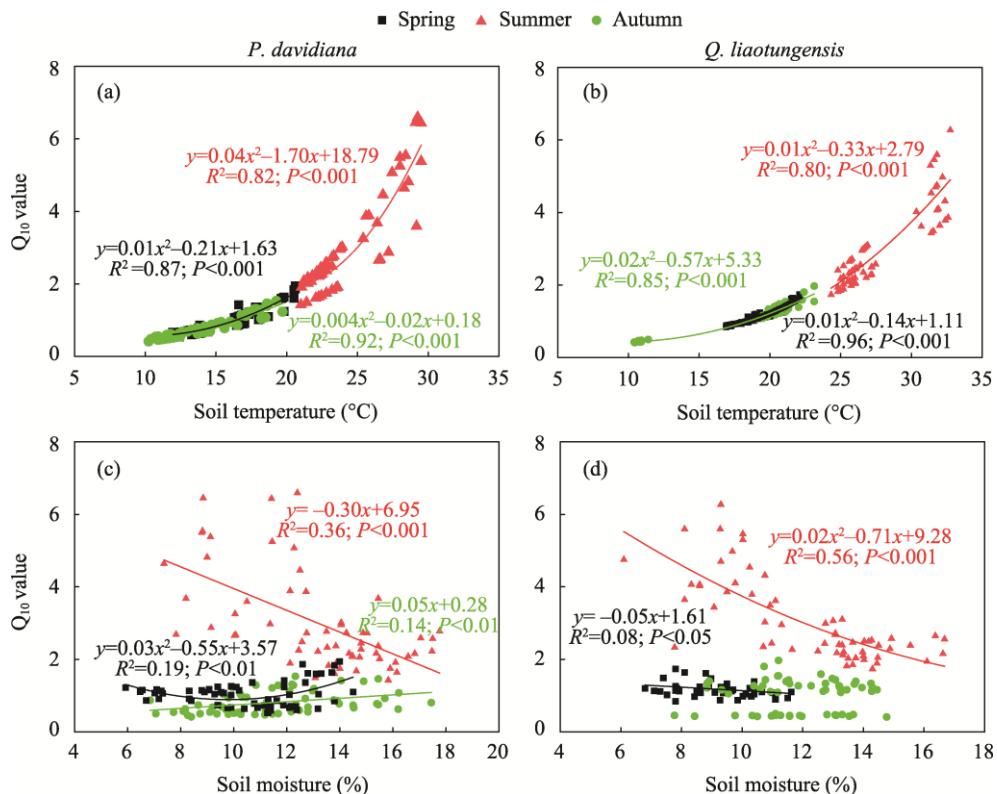


Fig. 4 Relationships of the Q_{10} of soil respiration with soil temperature and soil moisture in *P. davidiana* forests (a and c) and *Q. liaotungensis* forests (b and d)

Table 3 Litter biomass, litter carbon, fine root biomass, and root carbon in *P. davidiana* forests and *Q. liaotungensis* forests

Forests	Litter biomass (g/m ²)	Litter carbon (g/kg)	Fine root biomass (g/m ²)			Root carbon (g/kg)		
			Spring	Summer	Autumn	Spring	Summer	Autumn
<i>P. davidiana</i>	135.47 ±8.33 ^b	372.21 ±3.51 ^a	187.80 ±16.60 ^{Ba}	243.19 ±4.37 ^{Aa}	252.38 ±18.88 ^{Aa}	322.28 ±20.00 ^{Aa}	319.90 ±4.54 ^{Aa}	337.13 ±2.42 ^{Aa}
<i>Q. liaotungensis</i>	267.44 ±10.89 ^a	294.31 ±11.95 ^b	126.98 ±10.86 ^{Bb}	256.59 ±10.56 ^{Aa}	242.37 ±17.65 ^{Aa}	312.33 ±20.32 ^{Aa}	300.82 ±10.69 ^{Aa}	314.29 ±7.23 ^{Ab}

Note: Uppercase letters indicate the significant difference among different seasons ($P < 0.05$) and lowercase letters indicate the significant difference between different forests ($P < 0.05$).

Under different treatments, the Q_{10} values in *P. davidiana* forests were positively correlated with RB ($P < 0.05$; Fig. 5), and the Q_{10} values in *Q. liaotungensis* forests was only negatively correlated with LC for R_{total} and R_{no-litter} treatments ($P < 0.05$; Fig. 5b). The Q_{10} values in *P. davidiana* forests was negatively correlated with LB in summer ($P < 0.05$; Fig. 5c), and the Q_{10} values in *Q. liaotungensis* forests was significantly correlated with RB and LC in spring ($P < 0.05$; Fig. 5d).

3.4 Contribution of LB, RB, LC, and RC as well as soil temperature and soil moisture to the Q_{10} values

In structural equation model, the two forests showed strong relationships among soil temperature, soil moisture, and the Q_{10} values (Fig. 6). Among the examined plant characteristics, RB and LC can be effectively used to predict the Q_{10} values in *P. davidiana* forests (Fig. 6a and c). In addition, RB and LC had the greatest influence on the prediction of the Q_{10} values in *Q. liaotungensis* forests (Fig. 6b and d).

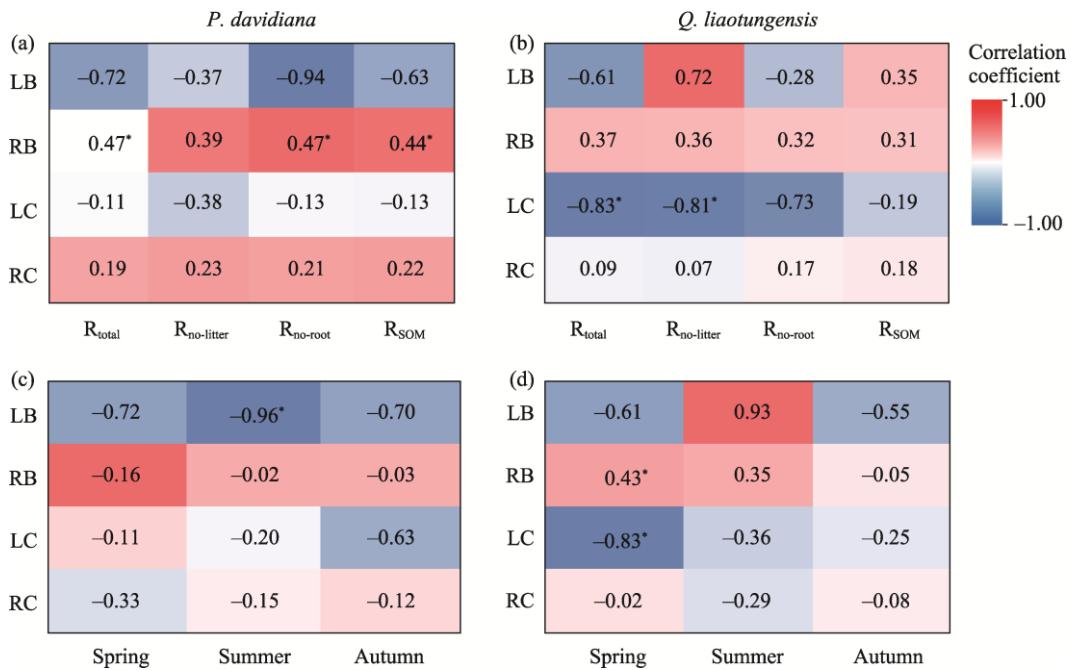


Fig. 5 Pearson correlation of the Q_{10} of soil respiration with litter biomass (LB), fine root biomass (RB), litter carbon (LC), and root carbon (RC) under different treatments and seasons. (a and b), the correlation of different treatments with LB, RB, LC, and RC; (c and d), the correlation of different seasons with LB, RB, LC, and RC. *, $P < 0.05$.

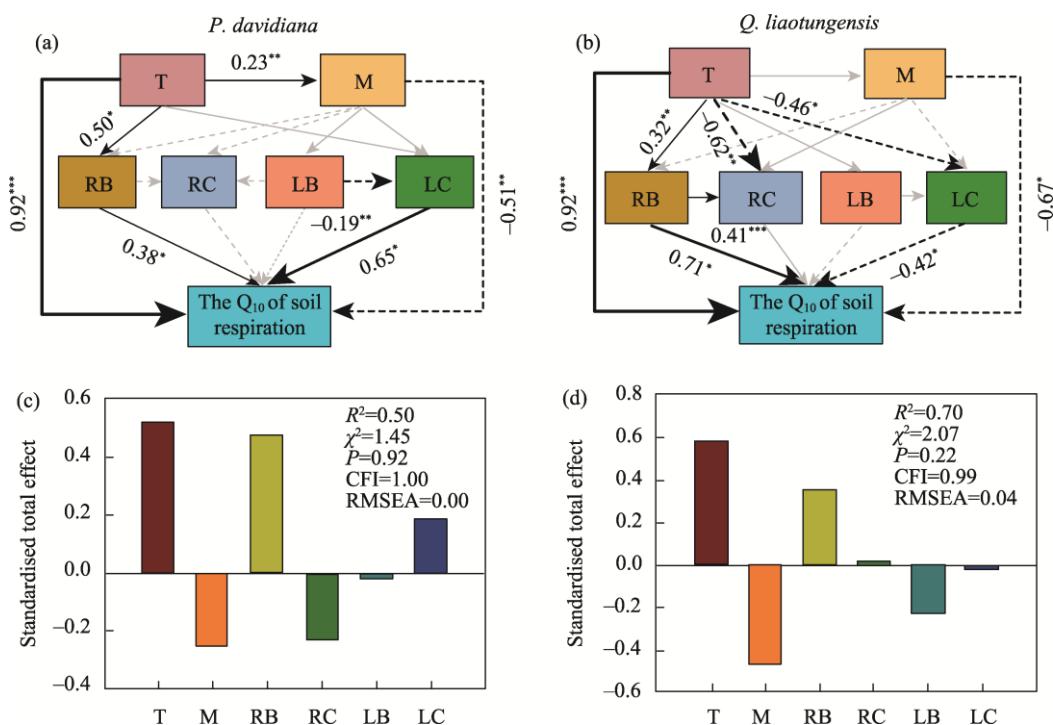


Fig. 6 Structural equation model for evaluating the direct and indirect effects of T, M, LB, RB, LC, and RC on the Q_{10} of soil respiration and standardised total effect in *P. davidianna* forests (a and c) and *Q. liaotungensis* forests (b and d). The black and grey lines indicate that the correlation is significant and not significant, respectively; the dashed and solid lines represent negative and positive correlations, respectively ($P=0.05$); and the line thickness represents the magnitude of the path coefficient. CFI, comparative fit index; RMSEA, root mean square error of approximation. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

4 Discussion

4.1 Effects of soil temperature and soil moisture on the seasonal dynamics of the Q_{10} of soil respiration

The Q_{10} of soil respiration showed strong seasonality (Fig. 1; Table 1). In both the forests, the highest Q_{10} values were observed in summer, and the lowest Q_{10} values were obtained in spring and autumn (Fig. 1). A higher Q_{10} value was obtained at higher temperature range mainly because the Q_{10} of unstable carbon mineralisation increased with temperature, and the metabolic efficiency of the microbial community was high (Wang et al., 2013). In spring and autumn, when the temperature was low, the activities of litter, root, and microbial respiration were weak, and the Q_{10} of soil respiration was mainly restricted by biochemical reactions (Wang et al., 2018). Therefore, the soil respiration rate was more sensitive to temperature in summer than that in spring and autumn, which indicated that an increase in temperature leads to an increase in carbon emission.

The Q_{10} of soil respiration between the two forests exhibited no significant difference ($P>0.05$; Fig. 1). The Q_{10} values were not significantly different in the two forests due to similar soil temperature and soil respiration (Kim et al., 2010). The insignificant differences also resulted from subtle changes in plant variables (root biomass and carbon content) between the two forests (Yan et al., 2013). In this study, the differences in plant characteristics were small, and the most variations between different forests were not obvious (Table 3). Therefore, above factors may be responsible for the insignificant difference between the Q_{10} values in *P. davidiana* forests and the Q_{10} values in *Q. liaotungensis* forests.

4.2 Effects of litter and root on the seasonal dynamics of the Q_{10} of soil respiration

The Q_{10} of soil respiration enhanced when the litter was included in soil respiration (especially in summer), because the Q_{10} values of R_{total} were significantly higher than that of $R_{\text{no-litter}}$. In addition, the Q_{10} values of $R_{\text{no-root}}$ were higher than that of R_{total} and $R_{\text{no-litter}}$ (Figs. 1 and 2), which further indicated that the litter enhanced the sensitivity of soil respiration to the temperature increase (Li et al., 2020, 2020c). Some studies have shown that the presence of litter leads to an increase in the substrate input, which increased microbial respiration and substances available for microorganisms (Li et al., 2016; Qu et al., 2018; Goncharova et al., 2020). Other studies also have shown different the Q_{10} values for R_a and R_h (Wang et al., 2017; Hu et al., 2018; Zeng et al., 2018). The interactions between litter decomposition and root activities led to an important impact on soil respiration (Subke et al., 2011; Wu et al., 2014), and the mechanism for the contact between the litter and root and soil respiration may be the microbial activities (Subke et al., 2011; Xiao et al., 2017). Due to the variations in availability of the two substrates of litter and root, the microbial decomposition activities led to the difference in soil respiration activities of various components of R_a and R_h (D'Acunto et al., 2018; Yan et al., 2018). Therefore, different major drivers of $R_{\text{no-litter}}$, $R_{\text{no-root}}$, and R_{SOM} as well as the asynchronous effects of these factors may lead to the variations in the Q_{10} of soil respiration (Wang et al., 2018; Li et al., 2020a, 2020c).

Due to the influence of environmental factors, root and microbial activities were weak in spring and autumn (Wang et al., 2018), and the Q_{10} values were low. In summer, compared with other treatments, $R_{\text{no-litter}}$ exhibited a low Q_{10} value ($P<0.05$; Fig. 1b), indicating that litter removal strongly affected the Q_{10} values (Kukumägi et al., 2017). The results from SEM supported this finding (Fig. 6). The results of the $R_{\text{no-root}}$ and R_{SOM} treatments are consistent with the temperature quality hypothesis reported in the literature (Suseela et al., 2013; Wu et al., 2014). Although missing roots exudate and the readily decomposable sources of carbon for microbes can influence soil respiration by affecting the decomposition of highly recalcitrant litter and soil organic matter (Wu et al., 2014; Kukumägi et al., 2017), long trenching experiments can change the soil conditions and microbial biomass and activity in the trenched plots (Kukumägi et al., 2017). Thus, the aforementioned factors can affect the Q_{10} values among various respiratory components. In addition, studies have reported the similar variations in the Q_{10} values (Jones et

al., 2005; Wu et al., 2014), which are consistent with the $R_{no-litter}$ results. The opposite results obtained for $R_{no-root}$ and $R_{no-litter}$ may be explained by labile carbon (Jones et al., 2005; Li et al., 2021). The $R_{no-litter}$ treatment allowed the root rhizosphere activity, thus permitting the input of labile carbon into the soil through photosynthesis (Wu et al., 2014). The $R_{no-root}$ treatment allowed litter input; however, a small amount of labile carbon entered the soil because trenching prevented root decomposition (Wu et al., 2014; Li et al., 2020b). The significant differences between $R_{no-litter}$ and R_{total} were due to the strong response of carbon input, microbial activities, and soil respiration under the co-existence of litter and root (Li et al., 2021). Therefore, the difference between $R_{no-litter}$ and R_{total} was large, especially in the long trench experiments (Jones et al., 2005; Li et al., 2020a). The Q_{10} values for $R_{no-litter}$ treatment were lower than that for other treatments in summer (Fig. 1), which indicated that the root activity reduced the Q_{10} values (Subke et al., 2011; Wu et al., 2014; Li et al., 2020b).

4.3 Driving factors of the variations in the Q_{10} of soil respiration

Soil moisture directly and indirectly affected both autotrophic and heterotrophic respiration through microbial as well as root physiological processes and oxygen and substrate diffusion, respectively (Aaltonen et al., 2017). In this study, soil moisture decreased during the rainy season (Fig. 2), which led to a significant increase in R_{total} , $R_{no-litter}$, $R_{no-root}$, and R_{SOM} (Aaltonen et al., 2017; Chen et al., 2019). The decreased soil moisture was beneficial to improve the oxygen utilisation rate of the soil (Aaltonen et al., 2017), which led to better plant growth and provided more carbon substrates for root respiration (Chen et al., 2019). Soil moisture exhibited a similar effect on the Q_{10} of soil respiration with higher substrate utilisation, which led to higher Q_{10} values (Brunner et al., 2015; Ferreira et al., 2016). When soil moisture decreased in summer, the soil moisture level was close to the optimal range required for microbial and root activities, which could increase the Q_{10} of soil respiration and components (Ferreira et al., 2016; Chen et al., 2019).

Moreover, soil temperature strongly affected the seasonal variations in the Q_{10} of soil respiration, and the seasonal variation in the Q_{10} values synchronises with soil temperature (Figs. 2 and 4). The correlation between soil temperature and the Q_{10} of soil respiration was stronger than that between soil moisture and the Q_{10} of soil respiration (Figs. 4 and 5). Soil temperature can be more important than soil moisture in influencing the Q_{10} of soil respiration in temperate forests (Xu et al., 2015). In addition, the Q_{10} of soil respiration was higher in summer than in spring and autumn, indicating that soil respiration was more sensitive to the temperature increase in warmer summers than in cooler spring and autumn (Fig. 2c and d). The Q_{10} values increased with an increase in temperature, which can be confirmed by the strong positive correlation between the Q_{10} of soil respiration and soil temperature (Figs. 4 and 5). The strong positive correlation between the Q_{10} of soil respiration and soil temperature can be explained as an increase in the enzyme activity with an increase in soil temperature (Kunito et al., 2018). The seasonal adaptation of the soil enzyme activity resulted from changes in isoenzymes, which adapt to the corresponding environmental temperature conditions (Di Nardo et al., 2004; Tucker et al., 2017; Guan et al., 2021). Thus, more relevant biological and biochemical activities were observed in summer (Qin et al., 2013).

From the comparison of different litter and root treatments, the Q_{10} of soil respiration can be enhanced without litter removal (Fig. 1). The LC exhibited a higher predictive capacity in *P. davidi* forests and *Q. liaotungensis* forests (Fig. 6a and b). Changes in LC affected the substrate availability of soil respiration, thereby influencing the Q_{10} of soil respiration (Meyer et al., 2018a; Yan et al., 2019). Litter decomposition can provide carbon that can be easily decomposed by microorganisms (Xu et al., 2018). However, the quantity and quality of litter varied with the forest types, which further affected soil carbon distribution and substrate quality for microbial respiration; therefore, LC exhibited different effects on the Q_{10} values in the two forests (Liu et al., 2017). Simultaneously, other plant characteristics played a role in the different Q_{10} values of respiration components in different forests. Among them, RB exhibited a strong predictive capacity for the Q_{10} values in *P. davidi* forests and *Q. liaotungensis* forests (Fig. 6).

because of the large seasonal duration (from spring to autumn) of root metabolism (Li et al., 2020b). Moreover, interactions between the root activity and soil organic matter may affect the variations in the Q_{10} values (Li et al., 2020a). With an increase in root death due to the trenching treatment, the respiration of root fragment decomposition increased, which may last until the second year (October 2016 to November 2018) and lead to an increase in the root respiration proportion (Wu et al., 2014; Kukumägi et al., 2017). Furthermore, the main predictors of the Q_{10} of soil respiration varied with seasons in different forests because of variations in tree species, ecosystem types, and experimental operation modes (Hu et al., 2016; Meyer et al., 2018b; Chen et al., 2019). Therefore, variations in the Q_{10} of soil respiration were affected by both the biological and abiotic factors (Hu et al., 2016).

5 Conclusions

The Q_{10} of soil respiration shows considerable seasonality in temperate forests, and the highest Q_{10} values are reached in summer. Among different soil respiration components, the litter enhances soil respiration. Compared with the litter effect, root have a lower CO_2 emission. In addition, *P. davidiana* forests and *Q. liaotungensis* forests have a similar Q_{10} of soil respiration. The interactions and synergistic effects of soil temperature, soil moisture, litter biomass, and fine root biomass play an important role in influencing the Q_{10} of soil respiration in the two forests. These results can explain how soil temperature, soil moisture, litter biomass, fine root biomass, litter carbon, and root carbon influence the Q_{10} of soil respiration and help us better understand how temperate forest systems respond to long-term climate dynamics.

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References

Altonen H, Lindén A, Heinonsalo J, et al. 2017. Effects of prolonged drought stress on Scots pine seedling carbon allocation. *Tree Physiology*, 37(4): 418–427.

Ballantyne A P, Andres R, Houghton R, et al. 2015. Audit of the global carbon budget: estimate errors and their impact on uptake uncertainty. *Biogeosciences*, 12(8): 2565–2584.

Bond-Lamberty B, Thomson A. 2010. Temperature-associated increases in the global soil respiration record. *Nature*, 464(7288): 579–582.

Bond-Lamberty B, Bailey V L, Chen M, et al. 2018. Globally rising soil heterotrophic respiration over recent decades. *Nature*, 560(7716): 80–83.

Brunner I, Herzog C, Dawes M A, et al. 2015. How tree roots respond to drought. *Frontiers in Plant Science*, 6: 547, doi: 10.3389/fpls.2015.00547.

Chang S X, Shi Z, Thomas B R. 2016. Soil respiration and its temperature sensitivity in agricultural and afforested poplar plantation systems in northern Alberta. *Biology and Fertility of Soils*, 52(5): 629–641.

Chen F, Yan G Y, Xing Y J, et al. 2019. Effects of N addition and precipitation reduction on soil respiration and its components in a temperate forest. *Agricultural and Forest Meteorology*, 271: 336–345.

Davidson E A, Janssens I A, Luo Y. 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10} . *Global Change Biology*, 12(2): 154–164.

D'Acunto L, Andrade J F, Poggio S L, et al. 2018. Diversifying crop rotation increased metabolic soil diversity and activity of the microbial community. *Agriculture, Ecosystems and Environment*, 257: 159–164.

Deng L, Liu G B, Shangguan Z P. 2014a. Land-use conversion and changing soil carbon stocks in China's 'Grain-for-Green' Program: a synthesis. *Global Change Biology*, 20(11): 3544–3556.

Deng L, Wang K B, Shangguan Z P. 2014b. Long-term natural succession improves nitrogen storage capacity of soil on the Loess Plateau, China. *Soil Research*, 52(3): 262–270.

Deng L, Wang K B, Zhu G Y, et al. 2018. Changes of soil carbon in five land use stages following 10 years of vegetation succession on the Loess Plateau, China. *CATENA*, 171: 185–192.

Di Nardo C, Cinquegrana A, Papa S, et al. 2004. Laccase and peroxidase isoenzymes during leaf litter decomposition of *Quercus ilex* in a Mediterranean ecosystem. *Soil Biology and Biochemistry*, 36(10): 1539–1544.

Ferreira A C C, Leite L F C, de Ara A S F, et al. 2016. Land-use type effects on soil organic carbon and microbial properties in a semi-arid region of northeast Brazil. *Land Degradation and Development*, 27(2): 171–178.

Gaumont-Guay D, Black T A, McCaughey H, et al. 2009. Soil CO₂ efflux in contrasting boreal deciduous and coniferous stands and its contribution to the ecosystem carbon balance. *Global Change Biology*, 15(5): 1302–1319.

Ge X G, Cao Y H, Zhou B Z, et al. 2020. Combined application of biochar and N increased temperature sensitivity of soil respiration but still decreased the soil CO₂ emissions in moso bamboo plantations. *Science of the Total Environment*, 730: 139003, doi: 10.1016/j.scitotenv.2020.139003.

Goncharova O, Matyshak G, Udovenko M, et al. 2020. Temporal dynamics, drivers, and components of soil respiration in urban forest ecosystems. *CATENA*, 185: 104299, doi: 10.1016/j.catena.2019.104299.

Guan C, Zhang P, Zhao C M, et al. 2021. Effects of warming and rainfall pulses on soil respiration in a biological soil crust-dominated desert ecosystem. *Geoderma*, 381: 114683, doi: 10.1016/j.geoderma.2020.114683.

He H L, Ge R, Ren X L, et al. 2021. Reference carbon cycle dataset for typical Chinese forests via colocated observations and data assimilation. *Scientific Data*, 8: 42, doi: 10.1038/s41597-021-00826-w.

Hu S D, Li Y F, Chang S X, et al. 2018. Soil autotrophic and heterotrophic respiration respond differently to land-use change and variations in environmental factors. *Agricultural and Forest Meteorology*, 250–251: 290–298.

Hu Y G, Jiang L L, Wang S P, et al. 2016. The temperature sensitivity of ecosystem respiration to climate change in an alpine meadow on the Tibet plateau: A reciprocal translocation experiment. *Agricultural and Forest Meteorology*, 216: 93–104.

Jones C, McConnell C, Coleman K, et al. 2005. Global climate change and soil carbon stocks: predictions from two contrasting models for the turnover of organic carbon in soil. *Global Change Biology*, 11(1): 154–166.

Kim D G, Mu S G, Kang S Y, et al. 2010. Factors controlling soil CO₂ effluxes and the effects of rewetting on effluxes in adjacent deciduous, coniferous, and mixed forests in Korea. *Soil Biology and Biochemistry*, 42(4): 576–585.

Kukumägi M, Ostonen I, Uri V, et al. 2017. Variation of soil respiration and its components in hemiboreal Norway spruce stands of different ages. *Plant and Soil*, 414(1–2): 265–280.

Kunito T, Shiroma T, Moro H, et al. 2018. Annual variation in soil enzyme activity in a paddy field: soil temperature and nutrient availability are important for controlling enzyme activities. *Applied and Environmental Soil Science*, doi: 10.1155/2018/4093219.

Lei N, Li J, Chen T Q. 2021. Respiration characteristics and its responses to hydrothermal seasonal changes in reconstructed soils. *Scientific Reports*, 11: 144, doi: 10.1038/s41598-020-80623-4.

Li J Q, Pendall E, Dijkstra F A, et al. 2020a. Root effects on the temperature sensitivity of soil respiration depend on climatic condition and ecosystem type. *Soil and Tillage Research*, 199: 104574, doi: 10.1016/j.still.2020.104574.

Li J Q, Pei J M, Pendall E, et al. 2020b. Spatial heterogeneity of temperature sensitivity of soil respiration: A global analysis of field observations. *Soil Biology and Biochemistry*, 141: 107675, doi: 10.1016/j.soilbio.2019.107675.

Li J Q, Nie M, Pendall E, et al. 2020c. Biogeographic variation in temperature sensitivity of decomposition in forest soils. *Global Change Biology*, 26(3): 1873–1885.

Li J Q, Pei J M, Dijkstra F A, et al. 2021. Microbial carbon use efficiency, biomass residence time and temperature sensitivity across ecosystems and soil depths. *Soil Biology and Biochemistry*, 154: 108117, doi: 10.1016/j.soilbio.2020.108117.

Li J W, Li M Y, Dong L B, et al. 2020. Plant productivity and microbial composition drive soil carbon and nitrogen sequestrations following cropland abandonment. *Science of the Total Environment*, 744: 140802, doi: 10.1016/j.scitotenv.2020.140802.

Li Y C, Hou C C, Song C C, et al. 2016. Seasonal changes in the contribution of root respiration to total soil respiration in a freshwater marsh in Sanjiang Plain, Northeast China. *Environmental Earth Sciences*, 75(10): 848, doi: 10.1007/s12665-016-5592-7.

Liu Y, He N P, Zhu J X, et al. 2017. Regional variation in the temperature sensitivity of soil organic matter decomposition in

China's forests and grasslands. *Global Change Biology*, 23(8): 3393–3402.

Liu Y L, Zhu G Y, Hai X Y, et al. 2020. Long-term forest succession improves plant diversity and soil quality but not significantly increase soil microbial diversity: Evidence from the Loess Plateau. *Ecological Engineering*, 142: 105631, doi: 10.1016/j.ecoleng.2019.105631.

Luan J W, Liu S R, Wang J X, et al. 2011. Rhizospheric and heterotrophic respiration of a warm-temperate oak chronosequence in China. *Soil Biology and Biochemistry*, 43(3): 503–512.

Ma Y C, Piao S L, Sun Z Z, et al. 2014. Stand ages regulate the response of soil respiration to temperature in a *Larix principis-rupprechtii* plantation. *Agricultural and Forest Meteorology*, 184: 179–187.

Machmuller M B, Ballantyne F, Markewitz D, et al. 2018. Temperature sensitivity of soil respiration in a low-latitude forest ecosystem varies by season and habitat but is unaffected by experimental warming. *Biogeochemistry*, 141(1): 63–73.

Meyer N, Welp G, Amelung W. 2018a. The temperature sensitivity (Q_{10}) of soil respiration: Controlling factors and spatial prediction at regional scale based on environmental soil classes. *Global Biogeochemical Cycles*, 32(2): 306–323.

Meyer N, Meyer H, Welp G, et al. 2018b. Soil respiration and its temperature sensitivity (Q_{10}): Rapid acquisition using mid-infrared spectroscopy. *Geoderma*, 323: 31–40.

Nelson D W, Sommers L E. 1982. Total carbon, organic carbon and organic matter. *Methods of Soil Analysis*, 9: 961–1010.

Qin J H, Zhang W X, Wang Q, et al. 2013. Temperature sensitivity of enzyme activity in subalpine forest soil in southwest China. *Acta Pedologica Sinica*, 50(6): 1241–1245. (in Chinese)

Qu L Y, Kitaoka S, Koike T. 2018. Factors controlling soil microbial respiration during the growing season in a mature larch plantation in Northern Japan. *Journal of Soils and Sediments*, 18(3): 661–668.

Rey A, Pegoraro E, Tedeschi V, et al. 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biology*, 8(9): 851–866.

Shi B K, Gao W F, Jin G Z. 2015. Effects on rhizospheric and heterotrophic respiration of conversion from primary forest to secondary forest and plantations in northeast China. *European Journal of Soil Biology*, 66: 11–18.

Subke J A, Voke N R, Leronni V, et al. 2011. Dynamics and pathways of autotrophic and heterotrophic soil CO_2 efflux revealed by forest girdling. *Journal of Ecology*, 99(1): 186–193.

Suseela V, Tharayil N, Xing B, et al. 2013. Labile compounds in plant litter reduce the sensitivity of decomposition to warming and altered precipitation. *New Phytologist*, 200(1): 122–133.

Todd-Brown K E O, Randerson J T, Post W M, et al. 2013. Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. *Biogeosciences*, 10(3): 1717–1736.

Tucker C L, McHugh T A, Howell A, et al. 2017. The concurrent use of novel soil surface microclimate measurements to evaluate CO_2 pulses in biocrusted interspaces in a cool desert ecosystem. *Biogeochemistry*, 135(3): 239–249.

Uri V, Varik M, Aosaar J, et al. 2012. Biomass production and carbon sequestration in a fertile silver birch (*Betula pendula* Roth) forest chronosequence. *Forest Ecology and Management*, 267: 117–126.

Varik M, Aosaar J, Ostonen I, et al. 2013. Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. *Forest Ecology and Management*, 302: 62–70.

Wang G B, Zhou Y, Xu X, et al. 2013. Temperature sensitivity of soil organic carbon mineralization along an elevation gradient in the Wuyi Mountains, China. *PLoS ONE*, 8(1): e53914, doi: 10.1371/journal.pone.0053914.

Wang K B, Deng L, Di D R, et al. 2020. Tracking soil carbon processes in two temperate forests at different successional stages using stable and radioactive carbon isotopes. *Agriculture, Ecosystems and Environment*, 304: 107143, doi: 10.1016/j.agee.2020.107143.

Wang M, Li X J, Wang S Z, et al. 2018. Patterns and controls of temperature sensitivity of soil respiration in a meadow steppe of the Songnen Plain, Northeast China. *PLoS ONE*, 13(9): e0204053, doi: 10.1371/journal.pone.0204053.

Wang Q K, Zhang W D, Sun T, et al. 2017. N and P fertilization reduced soil autotrophic and heterotrophic respiration in a young *Cunninghamia lanceolata* forest. *Agricultural and Forest Meteorology*, 232: 66–73.

Wang R, Wang Z Q, Sun Q Q, et al. 2016. Effects of crop types and nitrogen fertilization on temperature sensitivity of soil respiration in the semi-arid Loess Plateau. *Soil and Tillage Research*, 163: 1–9.

Wang R, Sun Q Q, Wang Y, et al. 2018. Contrasting responses of soil respiration and temperature sensitivity to land use types: Cropland vs. apple orchard on the Chinese Loess Plateau. *Science of the Total Environment*, 621: 425–433.

Wang R, Hu Y X, Wang Y, et al. 2019. Nitrogen application increases soil respiration but decreases temperature sensitivity:

Combined effects of crop and soil properties in a semiarid agroecosystem. *Geoderma*, 353: 320–330.

Wang T H, Yu S X, Cui G S. 2019. Impacts of climate change on global carbon cycle in ecosystem. *China Resources Comprehensive Utilization*, 37(1): 105–108. (in Chinese)

Wang W, Zeng W J, Chen W L, et al. 2013. Effects of forest age on soil autotrophic and heterotrophic respiration differ between evergreen and deciduous forests. *PLoS ONE*, 8(11): e80937, doi: 10.1371/journal.pone.0080937.

Wu C S, Zhang Y P, Xu X L, et al. 2014. Influence of interactions between litter decomposition and rhizosphere activity on soil respiration and on the temperature sensitivity in a subtropical montane forest in SW China. *Plant and Soil*, 381(1–2): 215–224.

Xiao H B, Li Z W, Dong Y T, et al. 2017. Changes in microbial communities and respiration following the revegetation of eroded soil. *Agriculture, Ecosystems and Environment*, 246: 30–37.

Xu L, Yu G, He N, et al. 2018. Carbon storage in China's terrestrial ecosystems: A synthesis. *Scientific Reports*, 8: 2806, doi: 10.1038/s41598-018-20764-9.

Xu Z F, Tang S S, Xiong L, et al. 2015. Temperature sensitivity of soil respiration in China's forest ecosystems: Patterns and controls. *Applied Soil Ecology*, 93: 105–110.

Yan J X, Chen L F, Li J J, et al. 2013. Five-year soil respiration reflected soil quality evolution in different forest and grassland vegetation types in the eastern Loess Plateau of China. *CLEAN-Soil, Air, Water*, 41(7): 680–689.

Yan T, Song H H, Wang Z Q, et al. 2019. Temperature sensitivity of soil respiration across multiple time scales in a temperate plantation forest. *Science of the Total Environment*, 688: 479–485.

Yan Z, Bond-Lamberty B, Todd-Brown K E, et al. 2018. A moisture function of soil heterotrophic respiration that incorporates microscale processes. *Nature Communications*, 9(1): 2562, doi: 10.1038/s41467-018-04971-6.

Yu S Q, Chen Y Q, Zhao J, et al. 2017. Temperature sensitivity of total soil respiration and its heterotrophic and autotrophic components in six vegetation types of subtropical China. *Science of the Total Environment*, 607–608: 160–167.

Zeng W J, Chen J B, Liu H Y, et al. 2018. Soil respiration and its autotrophic and heterotrophic components in response to nitrogen addition among different degraded temperate grasslands. *Soil Biology and Biochemistry*, 124: 255–265.

Zhang J J, Li Y, Wang J S, et al. 2021. Different responses of soil respiration and its components to nitrogen and phosphorus addition in a subtropical secondary forest. *Forest Ecosystems*, 8: 37, doi: 10.1186/s40663-021-00313-z.